

CLARIFICATION OF THE NESTING BEHAVIOUR OF *PODALONIA TYDEI SUSPICIOSA* (SMITH) (HYMENOPTERA: SPHECIDAE) BASED ON FURTHER OBSERVATIONS AT CASTLECLIFF BEACH, NEW ZEALAND

ANTHONY C. HARRIS

Otago Museum, PO Box 6202, Dunedin North, New Zealand

Abstract

Use of plant and dead animal material in the final stages of nest closure in *Podalonia tydei suspiciosa* (Smith) is recorded for 16 out of 17 nests studied. One individual used sand only to close the nest. Females cradled caterpillar prey with the forelegs. Female nesting behaviour, nests and cell size and shape were variable. Nests were made either before or after prey was captured. Nest cells were constructed in dry loose sand. All other sand-nesting solitary wasps nesting in the area constructed nest-cells in firm, moist sand. *Tachysphex nigerrimus* (Smith) (Larridae) competed with *P. t. suspiciosa* for nests, even usurping those of the latter, which it would then extend into firm, slightly moist sand. A number of mistakes in previous publications on the biology of *P. t. suspiciosa* are corrected.

Introduction

Podalonia tydei Fernald has a wide distribution in Southern Europe, Asia, North Africa, Australia and New Zealand, the subspecies *P. t. suspiciosa* (Smith) occurring only in Australia and New Zealand (Bohart and Menke 1976). Single-celled nests, containing one paralysed noctuid caterpillar, are made in loose sand.

Ethological data were summarised by Harris (2001) who, while primarily describing the larva, gave an account of nesting behaviour in *P. t. suspiciosa* on Castlecliff Beach (Wanganui, New Zealand), during late December 2000 to January 2001. In that study, females were not observed to cradle caterpillars, as had previously been observed in the Bay of Plenty (Harris 1994) and plant material was not used in nest closures, as had been reported by McCarthy (1917). Neither were females observed to use a stone to tamp down the nest closure, as had been reported in Australia by Chandler (1926), Bristowe (1971) and Rayment (1935). During the 2000-01 summer, my attention was at times diverted to other solitary wasps being studied and I sometimes interrupted final closure and disguising of the nest in order to more easily extract the prey and egg undamaged. Consequently, some details of final closure were probably missed.

The following summer, I revisited the Castlecliff sand dunes study area daily from 31 December 2001 until 31 January 2002. In this present study, 17 nests were observed until they were provisioned, closed and disguised and 32 prey items were observed being carried by females. Continuous, daily observations for a little over a month resolved some of the puzzling features of previous studies and provided a clear interpretation of the distinctive final closure of the nest.

Methods

Thirty-two individual wasps were followed and 17 burrows were excavated when nesting by the wasp was completed. All observations were recorded in field notebooks 57-60 (currently held by the author). Prey and eggs were placed on top of sand pressed into 35 mm plastic film canisters, which were placed into sealed jars filled with sand. The jars, with a thermometer beside them, were kept at 33-37°C on top of a hot water cylinder in a warming cupboard in a house, as described by Harris (2001). Larvae and prepupae were fixed in van Emden's larval fixative then stored in 75% ethanol.

All observations were made in the area of sand dunes at Castlecliff Beach, Wanganui, New Zealand, described by Harris (2001).

Observations and results

Mating

All matings observed resembled those described by Harris (1994).

Adult feeding

Adults took nectar frequently from flowers of catsear (*Hypochaeris radicata* Linnaeus), sweet alyssum (*Lobularia maritima* (Linnaeus) Desvaux) and cineraria (*Percallis x hybrida* R. Nordenstam).

Hunting and prey species

Hunting and prey species were as reported by Harris (1994, 2001). Final instar larvae of *Agrotis innominata* Hudson (Lepidoptera: Noctuidae) were taken and were abundant both in the areas where the wasps were nesting and where they were capturing prey.

Prey capture and paralysis

Prey capture and paralysis resembled that described by Harris (1994, 2001) except that two individuals, after stinging the prey to paralysis, subsequently bit and squeezed the area near the mouthparts and on the underside of the head and prosternum. The wasps may have been crushing the pharyngeal ganglia. One female appeared to feed from the prey's mouthparts, in the manner of a pompilid, but this may have been behaviour associated with crushing the pharyngeal ganglia and was most likely to prevent the caterpillar from disgorging a strong-smelling dark liquid from its mouth.

Prey carriage

In all cases, prey was held supine, facing forward, by the mandibles and cradled with the prothoracic legs, as described by Harris (1994) (Figs 1a-f). This was so for both large and small prey. No individual was observed to carry prey in the manner described by Harris (2001), except for one specimen, briefly, when it attempted to push a very large larva that it temporarily could not move. At that time, all its tarsi were in contact with the ground. During normal transport, mid legs alternately reach forward well beyond the forelegs, which tightly cradle the prey (Figs 1b, c, e, f).

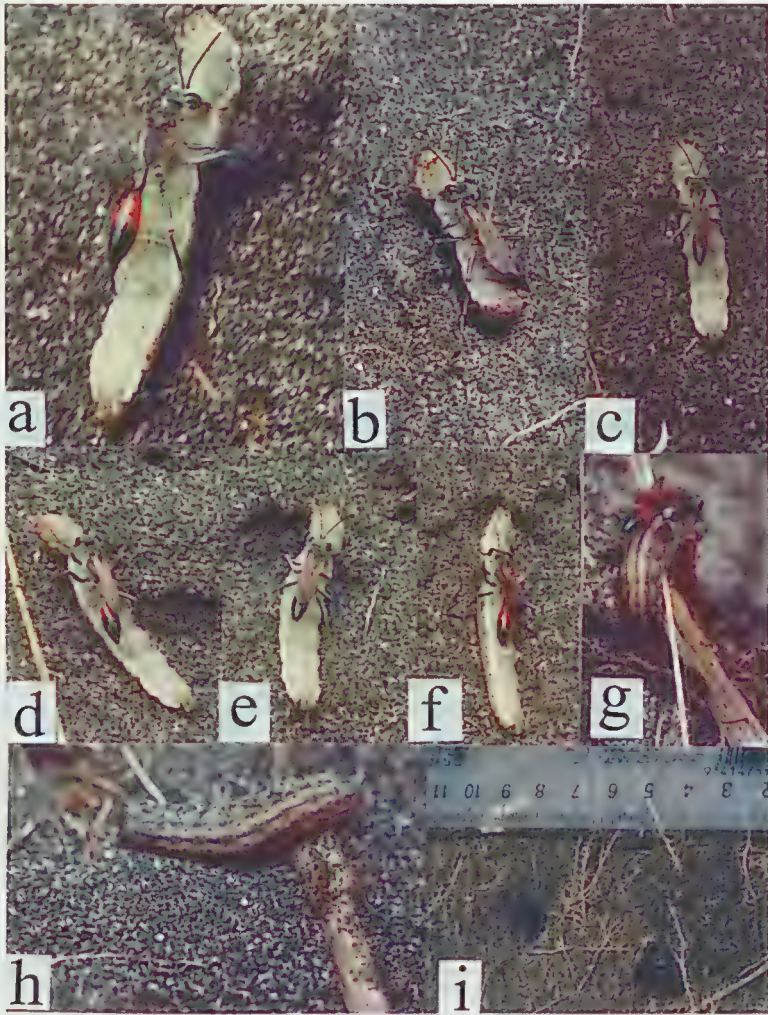


Fig. 1. Prey carriage by *P. t. suspiciosa*: (a), by beating its wings, this individual was able to move a large prey item rapidly; note that the prey is grasped by the mandibles and fore legs; normally, the wings remain folded over the wasp's back; (b), a smaller prey item; note how the wasp's right mid-leg reaches out forward of the fore leg, which grips the prey; (c), large prey carried in the typical manner; (d), prey is gripped by mandibles, forelegs move up to raise prey; (e), mid legs move over fore legs; (f), showing how the wasp balances on its mid and hind legs; (b, c, e & f) show typical prey carriage, cradled by forelegs; (g), positioning prey prone over an aerial root; (h), prey, placed prone over a plant stem, was partly covered with sand, then wasp visited a burrow dug the previous day; (i), two of the five closely-grouped burrows associated with this nest. Scale in mm, applicable only to (i).

Hiding prey

Wasps ran a few centimetres, then hung the caterpillar prone (dorsum up), never supine, over a leaf or a low plant, or over an exposed, horizontal root (Fig. 1g), or placed it under a leaf. When the caterpillar had been hung over a root or stem, some wasps would often turn away from it and kick sand over it with the forelegs, partially covering it with sand (Fig. 1h).

Abandonment of prey

Five paralysed, seemingly suitable prey were abandoned, supine, on warm sand during the study period. A sixth was abandoned when it expired after having been pushed into an area of intensely hot sand in front of the burrow.

Digging the nest

All nests were shallow, single-celled, dug with both the burrow and the terminal cell completely surrounded by dry, loose, sand. Additional burrows, and "false" burrows were dug as described by Harris (1994, 2001).

One individual dug 2 burrows on 9 January 2002 and a third burrow on 10 January. The wasp then captured and paralysed a final instar *A. innominata* caterpillar, hauled it forward with the mandibles and cradled by the forelegs, supine (venter up), and placed it twice, prone (dorsum up), on a horizontal root. The wasp ran back to the first nest it had made the previous day (9 January), then returned to the caterpillar, turned it supine and commenced dragging it towards this old burrow. It next hid the caterpillar, positioned prone under a leaf, 30 cm from the old burrow, to which it returned and started digging inside it for 13 seconds, presumably preparing a cell for the large prey (33.8 mm long). It then returned to the caterpillar and dragged it supine, head first into the mouth of the burrow and left it with the posterior abdominal segments exposed. The wasp then ran into the burrow under the caterpillar, which disappeared a few seconds later into the burrow.

The main burrow of all 17 nests excavated was 9-10.4 mm wide and 38-86 (mean: 64) mm deep, the cell being 17-56 (mean: 31) mm long. There were 2-6 "false" nests (Fig. 1i) as described by Harris (1994, 2001).

Orientation of prey within the nest

The caterpillar in the nest cell was sometimes coiled on its side in a "C" (sometimes a very loosely-coiled "C"), with the head and anus both facing the entrance. In two nests, the caterpillar was placed in the cell uncurled, supine and straight, with the head facing the end (apex) of the cell and the anus facing the nest entrance; part of the prey in these two nests extended out of the cell and along the main burrow (Figs 2a-d).

Oviposition

The egg (Fig. 3a) was laid laterally on the 2nd, 3rd or 4th abdominal segment. Exceptionally, one individual oviposited on the 1st abdominal segment.

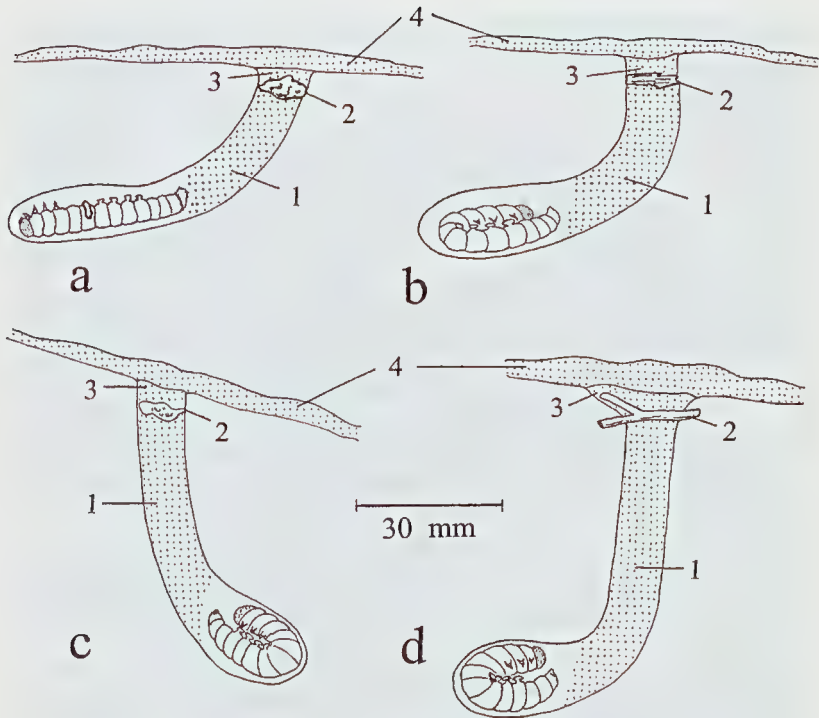


Fig. 2. Four nests of *P. t. suspiciosa* made in loose dry sand at Castlecliff Beach in January, 2002. Note that in (a), the prey is extended straight, whereas it is curled into a "C" in the other nests (b-d). In (d), a forked twig, of which the three points extended outside the diameter of the burrow, was positioned 7 mm below the mouth of the burrow and more sand kicked over that and compacted by the wasp with its frons. *Key to numbers:* 1, Initial sand closure. 2, Fragment of organic material. 3, Final sand closure. 4, Disguising sand kicked over burrow from several directions which camouflages the entrance and is not compacted with the front of the head.

Life history

Of 12 eggs on prey kept at 32-35°C, four subsequent larvae (Figs 3b-c) took six days to finish feeding and begin producing silk. (This constant high temperature is not attained in nature, where development is slower.) Pleural lobes were small in the final larva and large in the prepupa (Fig. 3c).

Nest closure

Between 63 and 76 seconds after entering the nest with the caterpillar (during which time oviposition on the caterpillar occurred), the female ran out 83-89 mm from the main entrance and, facing away from the burrow, kicked sand beneath itself with synchronous thrusts of the forelegs, the gaster being raised as sand passed beneath it then lowered.

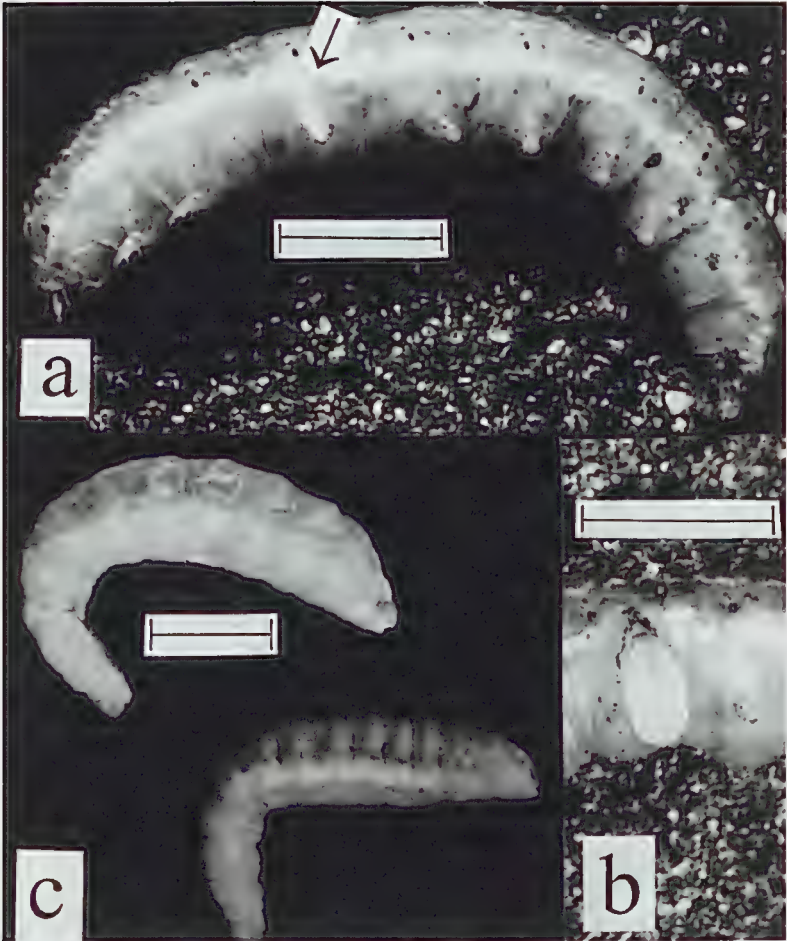


Fig. 3. Life history stages of *P. t. suspiciosa*: (a), egg; (b), first instar larva; (c), two mature larvae. In (c), the top larva has just finished eating its prey; the pleural lobes are small and rounded; the larva at bottom had just started producing its first 5 mm of silk; note that the pleural lobes are much larger. (Photographed 1 day after fixing in van Emden's larval fixative). All scale bars = 4 mm.

The wasp sent sand showering into the burrow for 8-11 seconds, then turned around, ran into the burrow and rammed sand with the front of its head (walking back and forwards, pushing sand with the front of its head and not vibrating its whole body) for about 8 seconds. Then the wasp reappeared, ran about 80 mm from the burrow entrance and, facing out, kicked in more sand beneath itself for about 6 seconds. Then it turned around, ran into the burrow

and rammed sand for about 4 seconds. It alternated between running out and kicking sand into the burrow for 4-16 seconds and turning around and rushing back to pound sand with its frons for 3-5 seconds. It made 8-17 (mean: 9) trips out and back. Each time, after the wasp had finished compacting sand with the front of its head inside the nest, it ran out backwards, pygidium first, the opposite way to a pompilid and many other solitary wasps which run out head first. As it dug, the meso- and metathoracic legs scrabbled to keep balance while the forelegs worked synchronously together, to scoop out sand and send it flying out under the gaster. As each shower of sand grains flew under the wasp, it raised then lowered its gaster, which bobbed continually up and down.

When the sand closure was about 7 mm from the surface, the female invariably ran out and looked for a small piece of dry stem, a leaf or similar organic object and placed it in the mouth of the burrow. It then ran out of the burrow, faced out and kicked in more sand beneath itself, turned around, ran back and compacted the sand with its head. When the sand closure reached the sand surface, the wasp disguised the nest for 77-86 seconds by sending sand showering over the nest from several directions, starting 142-157 mm from the burrow entrance (Fig. 2a-d).

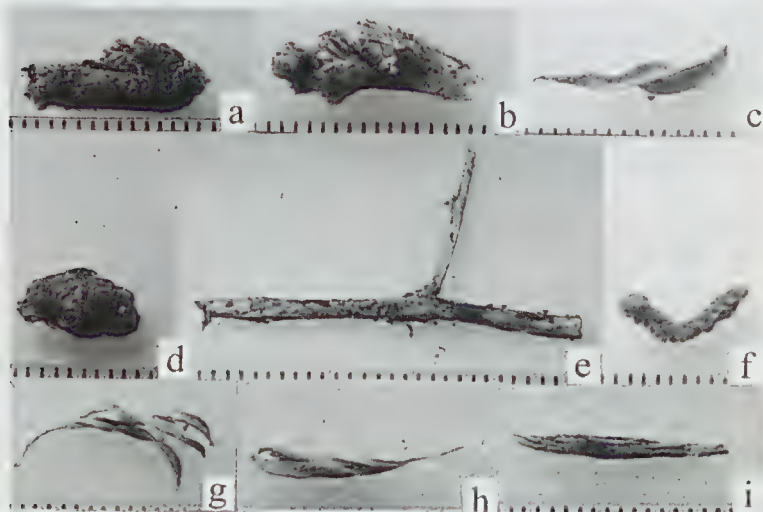


Fig. 4. Single items of organic material (a-i) from each of 9 nests of *P. t. suspiciosa*, positioned about 7 mm below burrow entrance. The wasp that placed item (d) in a nest seemed at first to be compacting soil with it, but inspection with a lens revealed that it was not. The same wasp used a forked twig, item (e), which was much wider than the diameter of the burrow, in its next nest. Items (a, b & d) are roundish wood, (c, g & h) are dried lupin leaflets, (i) is a piece of rotten wood and (f) is a hard, dried, lepidopterous caterpillar. All scales are in mm.

Organic material used in final closure of burrow

Only one individual did not use organic material (Figs 4a-i) to close its burrow. This individual finished closing its nest in light rain, which had caused surface sand to form a crust. The wasp excavated dry sand from beneath the crust and used this to complete its closure to the surface, sand alone being used to fill the nest (nest 17). In all other nests, except for the organic material near the entrance, the entire closure consisted of warm surface sand kicked into the burrow.

One individual, 7 mm below the burrow mouth, held a piece of marram grass rhizome and appeared to be about to ram sand with it (Fig. 4b). Close inspection with a lens revealed that it was, rather, positioning the material. The same female, in her next nest, chose a very thin, long, branching, Y-shaped twig 28 mm long (Fig. 4e). This twig was placed with its central part over the nest burrow, but its three ends were actually outside the nest burrow, so that it could not possibly be used to tamp down sand (Fig. 2d). The wood, moreover, was raised slightly above the sand inside the nest. The wasp ran back, turned away from the nest and kicked sand over the forked twig until it was buried, then tamped down sand with its head. It then ran out 93 mm from the nest and kicked sand over the area from several directions as it disguised the nest. Only one, seemingly token, piece of organic material was used in connection with each of the 16 completed nests observed in January 2002. These objects are listed in Table 1.

Table 1. Characteristics of organic material incorporated in nest closure.

Nest	Object
1	Ovoid marram grass rhizome fragment, 9 x 9 mm
2	Marram grass rhizome fragment, 9 mm x 5 mm (Fig. 4d)
3	Forked twig, 28 mm long (Fig. 4e)
4	Rotten wood fragment, 16 mm x 1.8 mm (Fig. 4i)
5	Dead wood fragment, 13.5 mm x 6 mm (Fig. 4a)
6	Dried, diseased lupin leaf shoot, 14 mm long (Fig. 4g)
7	Dead, dry, hard, <i>Agrotis innominata</i> (?) early instar larva, 14 mm long (Fig. 4f)
8	Marram grass rhizome fragment, resembling that in nest 1
9	Lupin leaf fragment, 14 mm long (Fig. 4c)
10	Lupin leaf fragment, 18 mm long (Fig. 4h)
11	Wood fragment, 17 mm x 8.2 mm (Fig. 4b)
12	Marram grass rhizome fragment, 9 mm x 6 mm
13-16	Marram grass rhizome fragment resembling that in nest 2
17	No organic material used; nest filled entirely with dry sand taken from beneath hard, crusted sand after light rain had commenced

Compacting of nest closure without a "tool"

In the burrow entrances, females were not observed to ram by holding a pebble in the mandibles while vibrating the whole body with rapid and audible movement of the flight muscles. It is concluded that, at least on coastal beaches in the Bay of Plenty and at Castlecliff Beach in New Zealand, this species does not use a "tool" to ram nest material. Instead, it drops a piece of dry organic material on the sand of the nest closure about 7 mm from the surface and then puts more sand on top of it.

Variability of nidification cycle

This species sometimes digs its nest before hunting for prey and, at other times, digs its nest after finding prey. In the 2002 observations, no individual was seen to take prey into a succession of burrows before finally ovipositing on the prey, as was recorded by Harris (2001), indicating that this is a variable aspect of nidification behaviour. There were, nevertheless, many variations in the manner in which the paralysed larvae were taken to the nest, including long detours and partial burial of the prey. The unpredictability of which burrow is finally chosen as the nest, together with the placement of organic material within the burrow, about 7 mm below its mouth, possibly make it more difficult for potential predators to locate the immature wasp.

The caterpillar in the nest cell was often coiled on its side (sometimes very loosely) in a "C", with the head and anus both facing the entrance. In two nests, the caterpillar was placed in the cell supine, uncurled and straight, with the head facing the end (apex) of the cell and the anus facing the cell entrance. The egg was placed on the 2nd abdominal segment on both of these non-curved prey. Both nests were very shallow, one being 38.3 mm deep.

Competition

Three *Tachysphex nigerrimus* (Smith) (Larridae) females were observed to drive *P. t. suspiciosa* females from nests. On 7 January 2002, a *P. t. suspiciosa* female spent 38 minutes digging a burrow 63 mm deep, then walked, orienting, around the nest area. As it was doing this, a *T. nigerrimus* female ran into the burrow and remained inside. The *P. t. suspiciosa* female ran into its burrow, ran out, then in and out again twice, after which the *T. nigerrimus* female flew out, rushed at the *P. t. suspiciosa* and drove it away, then re-entered the usurped burrow. The *P. t. suspiciosa* returned, faced away from the burrow and started digging sand into the burrow and ramming it with its head. The *T. nigerrimus* ran out through the sand, flew at the *P. t. suspiciosa*, then began removing sand that the latter had kicked into the burrow. The *T. nigerrimus* female then extended the burrow into firm, slightly damp sand while the *P. t. suspiciosa* began digging a new burrow 14 cm away from its usurped burrow. After 26 seconds, the *P. t. suspiciosa* abandoned her second burrow and ran into the *Acacia longifolia* var. *sophorae* scrub. Two further *T. nigerrimus* females drove *P. t. suspiciosa* females from their burrows but did not nest in the usurped burrows (field notebook 57).

Discussion

Observations made during this and earlier studies are summarised in Table 2. Evan's (1964) assertion that 'all Sphecinae pack the nest closure with blows of the head, while other Sphecidae use the pygidium for this purpose,' is true for *P. t. suspiciosa*. The behaviour seen repeatedly in January 2002 somewhat resembled McCarthy's (1917) brief account of its nidification in Australia, except that New Zealand individuals never used increasingly larger soil particles as they approached the surface, only sand being used, apart from the single item of organic material used about 7 mm from the surface. In all my studies of 1992, 2001 and 2002, no individual rammed sand by holding a small chip in her mandibles 'like a tool', as was described for *P. t. suspiciosa* in Australia by Chandler (1926), Bristowe (1971) and Rayment (1935). When nesting in soil other than marine sand, females may well tamp soil with a chip, but this has not been observed in New Zealand.

Table 2. Summary of observations.

Observations

Prey carriage normally resembles that described by Harris (1994).

Prey is sometimes crushed or lapped around the mouth or oesophagus with the wasp's mandibles and other mouthparts, possibly crushing the host's oesophageal ganglia and imbibing the host's fluids (2 observations).

Prey is caught either before or after construction of the nest.

The prey may be placed in the burrow on its side, curved into a "C", with both head and anus facing the entrance, or (rarely) it may be positioned supine, extended straight, non-curved, with its head facing the end wall (apex) of the cell and with its anus facing the entrance or projecting up the burrow.

The wasp's egg is positioned laterally on the prey, between the 1st and 4th abdominal segment, usually on the 2nd, 3rd or 4th.

Nests are always single-celled.

There are several, very closely-grouped burrows, usually 2-7.

Prey on occasion may seemingly be placed in any one of the 2-7 grouped burrows and, at times, in a nest dug elsewhere.

The entire nest, including both burrow and cell, is completely surrounded by dry, loose sand.

Burrows are filled by sand, kicked by the fore legs below the wasp, facing away from the nest and compacted by ramming with the front of the wasp's head, the wasp alternating between digging and compacting every 3-8 seconds.

During burrow closure, the wasp exits the burrow backwards, pygidium first. Many other solitary wasps, including Pompilidae, exit the burrow head first.

A piece of dry organic matter, varying from a tiny scrap of rotten wood to a twig, a dried leaf, a sprig of dried leaves and a hard, dried, lepidopterous caterpillar, is usually placed in the sand fill of the burrow about 7 mm below the mouth, then more sand is placed on top until the surface is attained, when the nest is disguised.

The nest closure is not tamped down by an object held in the mandibles.

O'Brien (1983) stated that *Podalonia argentifrons* (Cresson), in Arizona, placed a noctuid larva in its burrow not rolled into a "C" shape, but extended out straight, lying on its right side. An egg was placed laterally on the left side between the third thoracic and the first abdominal segments. O'Brien (1983) stated that the non-curved position of the prey might be species-specific to *P. argentifrons*, because 'so far as is known, all cutworms stored by *Podalonia* Fernald species are curled in a "C" shape.' However, my observations of March 1992 and January 2002 indicate that *P. t. suspiciosa* occasionally also places prey in the burrow in an extended, non-curved position, often when it has an exceptionally large prey item, at which times the prey may extend out of the cell and into the burrow.

Evans (1987) stated that *Podalonia occidentalis* Murray was 'unusually variable' in many aspects of its behaviour. Thus nests and prey were both sometimes aborted, some nests were filled with quarries and others lacked quarries (a quarry being an auxiliary burrow dug near the nest for the purpose of obtaining spoil to close the nest burrow). Egg position also varied considerably. The most striking variation in *P. occidentalis* was in the nest-prey dichotomy, this behavioural difference often being considered a fundamental one (Evans 1987). Most reported accounts of *Podalonia* species (and many other more generalised wasps) take prey before they make a nest. In contrast, more derived or specialised wasps (e.g. *Ammophila* W. Kirby) take prey only after they have made a nest (Evans and West-Eberhard 1970, O'Neil 2001, Iwata 1942, 1976).

Evans (1987) stated that an unusual amount of variation in nesting behaviour has been reported in at least two other species of *Podalonia*. He stated that *P. valida* (Cresson) is distinctive in that females make a series of nests in a restricted territory that is defended against intrusion by other females and there was evidence that *P. occidentalis* females return again and again to the same general area to nest, without exhibiting territorial behaviour. In my 2002 observations, *P. t. suspiciosa* behaved on occasions like *P. occidentalis* and *P. valida*, returning to the same general area to nest (always without territorial behaviour). It usually made a series of tightly grouped false burrows.

In 2002, *P. t. suspiciosa* females were thrice observed to be driven from burrows they had dug by the smaller *Tachysphex nigerrimus* females, which then usurped the burrows, either modifying them for their own use or subsequently abandoning them. *P. t. suspiciosa* females at Castlecliff Beach were not limited by scarce nesting space. It is possible that *P. t. suspiciosa* females would compete inter-specifically for nesting territory if they were restricted, in the same way that females of the pompilid wasp *Priocnemis* (*Trichocurgus*) *conformis* Smith fight ferociously for nesting space on Leith Saddle, Dunedin, where nesting space is limited. In my experience, this occurs nowhere else, at least not to the same extent (Harris 1999).

Evans (1987) stated that *Podalonia* appears to be a genus in transition, with respect to whether the prey is taken before nest building or after the nest is built. Similarly, O'Neill (2001) stated that it is uncertain whether *Podalonia* species represent primitive forms in the evolution of sphecoid nesting behaviour, or whether they have secondarily reverted to a primitive form of nesting (a change in the nesting hierarchy from stage 4a, nest-prey-egg-closure, to stage 3, prey-nest-egg-closure). Nesting cycles are represented by formulae, arranged in an hierarchy that may represent an evolutionary sequence of behaviour (e.g. Harris 1987, 1994, 1999). The second of O'Neil's (2001) alternatives appears to best fit the behaviour of *P. t. suspiciosa* in New Zealand. O'Neil (2001) further suggested that *Podalonia* species may change from stage 3 to stage 4a, depending on prey availability, but this certainly did not apply at Castlecliff Beach where the prey, *Agrotis innominata* final instar larvae, were at all times abundant in the study area.

Acknowledgements

I am very grateful to Mrs E.C. Harris for assistance with all aspects of this work and Mr A.W. Don and Ms A. Jul for commenting on an earlier draft of the manuscript.

References

- BOHART, R.M. and MENKE, A.S. 1976. *Sphecoid wasps of the world: a generic revision*. University of California Press, Berkeley; 695 pp.
- BRISTOWE, W.S. 1971. The habits of a West Australian sphecoid wasp. *Entomologist* **104**: 42-44.
- CHANDLER, L.G. 1926. Habits of the sand-wasp. *Victorian Naturalist* **42**: 107-114.
- EVANS, H.E. 1964. The classification and evolution of digger wasps as suggested by larval characters (Hymenoptera: Sphecoidea). *Entomological News* **9**(75): 225-237.
- EVANS, H.E. 1987. Observations on the prey and nests of *Podalonia occidentalis* Murray (Hymenoptera: Sphecidae). *Pan-Pacific Entomologist* **63**(2): 130-134.
- EVANS, H.E. and WEST-EBERHARD, M.J. 1970. *The wasps*. University of Michigan Press, Ann Arbor; 265 pp.
- HARRIS, A.C. 1987. Pompilidae (Insecta: Hymenoptera). *Fauna of New Zealand* **12**. Department of Scientific & Industrial Research, Wellington; 154 pp.
- HARRIS, A.C. 1994. Sphecidae (Insecta: Hymenoptera). *Fauna of New Zealand* **32**. Landcare Research, Lincoln; 111 pp.
- HARRIS, A.C. 1999. The life histories and nesting behaviour of the Pompilidae (Hymenoptera) in New Zealand: a comparative study. *Species Diversity* **4**(1): 143-235.
- HARRIS, A.C. 2001. Nesting behaviour of *Podalonia tydei suspiciosa* (Smith) (Hymenoptera: Apoidea: Sphecidae: Sphecinae) at Castlecliff Beach, Wanganui, with a description of the mature larva. *New Zealand Entomologist* **24**: 57-62.
- IWATA, K. 1942. Comparative studies on the habits of solitary wasps. *Tenthredo* **4**: 1-146.
- IWATA, K. 1976. *Evolution of instinct: comparative ethology of Hymenoptera*. Amerind Publishing Co., New Delhi; 535 pp. (Translation of 1971 Japanese edition).
- MCCARTHY, T. 1917. Some observations on solitary wasps at Hay, N.S.W. *Australian Naturalist* **3**(15): 195-200.
- O'BRIEN, M.F. 1983. Observations on the nesting of *Podalonia argentifrons*. *The Southwest Entomologist* **8**(3): 194-197.
- O'NEILL, K.M. 2001. *Solitary wasps, behaviour and natural history*. Comstock Publishing Associates, Cornell University Press, Ithaca; 406 pp.
- RAYMENT, T. 1935. *A cluster of bees*. The Endeavour Press, Sydney; 750 pp.